

Optimal reproductive-skew models fail to predict aggression in wasps

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Optimal-skew models (OSMs) predict that cooperative breeding occurs as a result of dominants conceding reproductive benefits to subordinates, and that division of reproduction within groups reflects each cooperator's willingness and ability to contest aggressively for dominance. Polistine paper wasps are a leading model system for testing OSMs, and data on reproduction and aggression appear to support OSMs. These studies, however, measure aggression as a single rate rather than by the activity patterns of individuals. This leads to a potential error: if individuals are more likely to receive aggression when active than when inactive, differences in aggression across samples can reflect changes in activity rather than hostility. This study replicates a field manipulation cited as strongly supporting OSMs. We show that fundamentally different conclusions arise when controlling for individual activity states. Our analyses strongly suggest that behaviours classified as 'aggression' in paper wasps are unlikely to function in establishing, maintaining or responding to changes in reproductive skew. This illustrates that OSM tests using aggression or other non-reproductive behaviour as a metric for reproductive partitioning must demonstrate those links rather than assume them.

Keywords: aggression; cooperation; *Polistes*; reproductive skew; social wasps

1. INTRODUCTION

A common feature of cooperatively breeding groups is reproductive skew, where behaviourally dominant group members leave more direct offspring than do subordinate members (Vehrencamp 1983; Keller & Reeve 1994). The degree to which dominants monopolize reproduction may be tempered by the subordinates' threats to either leave the group or aggressively contest for dominance status. If cooperation is indeed facultative across all group members, then the evolution of stable cooperative groups may involve reproductive 'transactions' between members. Such 'optimal-skew' models (OSMs) predict that dominants and subordinates reach a reproductive compromise that gives subordinates enough direct reproduction to at least equal their expected fitness from being solitary (Reeve 1991, 2000; Reeve & Ratnieks 1993; Reeve *et al.* 1998a; Johnstone 2000).

The OSM framework has two general predictions. The first is that reproduction is often shared between dominants and subordinates. The quantitative skew is potentially affected by multiple variables, including: the intrinsic abilities of dominants and subordinates to contest or appropriate reproduction; the genetic relatedness between group members; the ecological constraints on solitary reproduction and switching between groups; and the group productivity benefits resulting from each added subordinate (Johnstone 2000). Owing to this multiplicity of variables, quantitative predictions are difficult. For example, greater genetic relatedness may predict either increased or decreased skew, depending on whether dominants or subordinates primarily control reproductive

allocation (Reeve & Keller 2001). Thus, the same observed pattern of reproductive skew could be interpreted as not supporting an OSM (e.g. Field *et al.* 1998; Queller *et al.* 2000) or as strongly supporting an OSM (e.g. Reeve & Keller 2001). Furthermore, tests of OSM models may fail to predict reproductive-skew patterns because they neglect to include constraints such as mate choice (Haydock & Koenig 2002), costs such as inbreeding (Cooney & Bennett 2000; Clutton-Brock *et al.* 2001) or delayed benefits such as gaining a valuable territory in the future (Kokko & Johnstone 1999; Ragsdale 1999). Indeed, definitive interpretations of quantitative reproductive data may first require confirmation of which set of assumptions apply to the species being considered (Clutton-Brock 1998; Magrath & Heinsohn 2000).

The second prediction of OSMs is that aggression is a primary mechanism for setting the reproductive skew, by demonstrating the interactants' ability and willingness to contest reproduction, or for responding to reproductive cheating by group members. For the same reasons as above, quantitative predictions about aggression levels depend critically on a group's social and ecological context. For example, without specifying the context one cannot predict whether close kin should be the most or least aggressive towards each other (Cant & Johnstone 2000). Nevertheless qualitative changes in aggression can be used to test OSMs. If aggression is tied to reproductive skew, then changes in skew should produce changes in aggression. Hence, the first experimental tests of an OSM disrupted an existing pattern of reproduction (Reeve & Nonacs 1992, 1997). Depending on which offspring were affected, different patterns of changes in aggression by dominants and subordinates were predicted. The close match between prediction and observation in those experiments remains to this day one of the strongest sources of

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support for OSMs (Keller & Reeve 1994; Reeve *et al.* 1998a, 2000; Keller & Chapusiat 1999; Reeve & Keller 2001).

The experiments of Reeve & Nonacs (1992, 1997) looked at cooperation between colony foundresses in the paper wasp, *Polistes fuscatus*. Nest-mate foundresses are 'aggressive' in many *Polistes* species, as evidenced by multiple darts, lunges and bites at each other. Although in stable associations these interactions rarely escalate to fights and injuries, their commonness strongly suggests an adaptive function. Therefore, when reproductive skew was manipulated by removing eggs destined to become reproductive gynes and males, both dominant and subordinate wasps were predicted and observed to increase their rates of aggression, the subordinate significantly more so. The initial evolutionary explanation for these reactions was that removal of these eggs affects subordinate direct fitness relatively more than dominant direct fitness (Reeve & Nonacs 1992, 1993). This assumed that subordinates produce a significant fraction of reproductively destined eggs, but later results found that dominants produce almost all these eggs (Reeve *et al.* 2000). Thereafter, the increase in subordinate aggression was attributed to a greater inclination to compete for laying opportunities (Reeve & Keller 2001). However, because subordinates were not observed to lay eggs, the existence of reproductive competition remains open to question. Questions such as this led us to replicate the main experiment of removing reproductively destined eggs. In this new experiment we also recorded data on activity patterns and genetic relatedness that were not available in previous experiments. Therefore, the replicated experiment is a far stronger test of whether aggression patterns are supportive of OSMs.

2. METHODS

(a) *Field site and data collection*

The study species was again *P. fuscatus*. We conducted this study in the summers of 1996 and 1997 in Ithaca, NY, USA. Across both seasons, we manipulated double ($n = 15$), triple ($n = 2$) and quadruple ($n = 2$) foundress nests ($n = 19$ dominants and 25 subordinates). In *P. fuscatus* dominants are generally larger, more active in initiating darts, lunges and bites, exhibit mounting behaviour (standing on top of a wasp and chewing on its back), leave the nest less frequently, gather wood pulp rather than food and lay the majority or all of the eggs. The high correlation (Reeve 1991; Reeve & Nonacs 1992, 1997; Reeve *et al.* 2000; Tibbetts & Reeve 2000) across these characters allows identification of the dominant wasp usually within 1–2 h of observation. All study nests were located by early June, and the wasps were weighed to the nearest milligram and uniquely marked with paint spots. In late June or early July we videotaped each nest for at least 2 h (between 10.00 and 13.00, when wasps begin to forage) (the 'before' measurement). The next morning, we captured the wasps, took down the nests, removed all eggs, replaced the nests and returned the wasps. We then videotaped each nest for 2 h, again usually between 10.00 and 13.00 (the 'after' measurement). Occasionally, the morning of the manipulation remained colder than the previous day. Because wasp activity levels are affected by temperature (Tibbetts & Reeve 2000), we waited until either the afternoon or the following morning to take the 'after' measurement. Thus all nests were

measured at approximately equal ambient temperature (± 3 °C) if not at the same time of day.

(b) *Behavioural analyses*

All videotapes were analysed by P.N. without knowledge of nest identity or presence of eggs. The activity of each wasp on a nest was categorized as inactive, grooming, nest constructing, walking, cell inspecting (similar to walking but clearly putting a head into a cell), mounting or laying an egg. Once a wasp commences laying it becomes motionless and appears inactive. Grooming and nest constructing involve obvious activity, but not movement across the face of the nest. Walking and cell inspecting are the most active behaviours and generally involve travelling across the nest. An activity profile was generated for each wasp detailing the total time spent in each activity state and the number of bouts of each activity. Aggression was categorized as antennation, dart, lunge, bite or mount (see Gamboa *et al.* (1986) and Reeve & Nonacs (1992, 1997) for full descriptions of each act). For each aggressive act we recorded the identities of both the initiator and the recipient and their activity states at the time. For statistical analyses, we calculated weighted aggression rates per minute that a pair of wasps spent on the nest together. Darts were weighted by a factor of two, and each lunge and bite by a factor of three. Mounts are considered reliable indicators of dominance and categorized at the higher end of the spectrum of aggressive acts (Gamboa *et al.* 1986; Tibbetts & Reeve 2000). Therefore, we gave them the maximum weighting of four. Antennation has been considered a tolerant rather than aggressive behaviour (Gamboa *et al.* 1986). We include antennation in aggression for two reasons: (i) it often precedes and is involved in mounting (P. Nonacs, H. K. Reeve and P. T. Starks, personal observation); and (ii) it was the only individual act whose rate increased (although not significantly) after the manipulation. Therefore, the combination of including antennation and differentially weighting each type of act maximizes the probability of finding significant increases in aggression (i.e. as found in our previous studies and predicted as the proximate mechanism in OSMs).

Weighted aggression reflects an increase in presumed severity of each event, and therefore analyses have greater power to either detect changes in aggression rates or shifts from less to more aggressive acts (i.e. a decrease in tolerance; Gamboa *et al.* 1986). Nevertheless, giving behavioural differential weightings adds a subjective element to the data analyses. Therefore, analyses were repeated with unweighted rates and overweighted rates (i.e. darts, lunges and mounts weighted by factors of three, six and nine, respectively). These results did not differ in any substantive way and therefore are omitted for brevity.

(c) *Genetic analyses*

Genomic DNA from the thoraces or legs of 16 individuals ($n = 8$ colonies) was extracted using Qiagen extraction kits. Samples were amplified as in Reeve *et al.* (2000) and visualized on an Applied Biosystems ABI Prism 377 DNA sequencer in the University of California, Integrative Biology genetics facility. Gel files were analysed using the SEQUENCING ANALYSIS and GENOTYPER v. 2.5 programs, and relatedness estimates were calculated from the nine polymorphic microsatellite loci (PACO3219, PACO3155, Pbe128, Pbe203, Pbe411, Pbe424, Pbe440, Pbe442 and Pbe102; 5.4 ± 0.7 alleles per locus) using RELATEDNESS v. 5.0.8 (Goodnight & Queller 1994). The primers used to amplify the microsatellites were designed by Strassmann *et al.* (1996, 1997). Unfortunately, the specimens from the

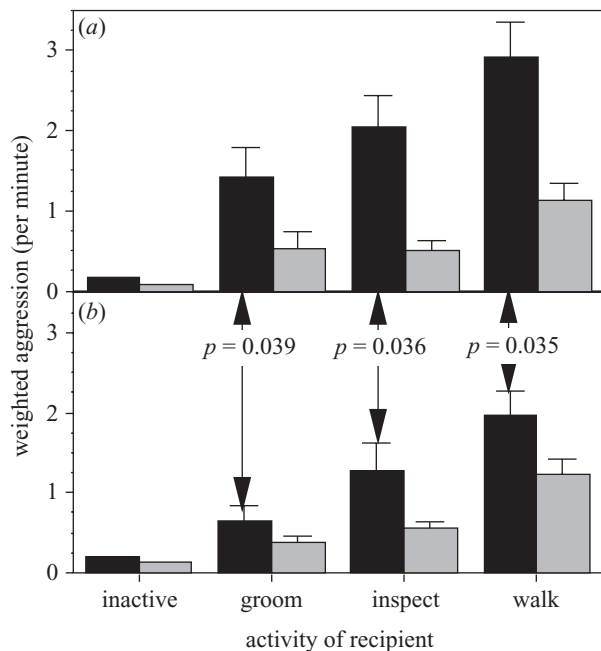


Figure 1. Weighted aggression rates (+s.e.) split by the activity of the recipient wasp. Two-factor repeated-measures ANOVAs find that dominants (black bars) are significantly more aggressive than subordinates (grey bars) both (a) before ($F_{1,43} = 13.46$, $p < 0.001$) and (b) after ($F_{1,48} = 5.78$, $p = 0.020$) the egg removal, and that the activities (the repeated measure) differ significantly in stimulating aggression (a) before ($F_{3,129} = 32.28$, $p < 0.0001$) (a) and (b) after ($F_{3,144} = 34.62$, $p < 0.0001$) egg removal. Matched-pair t -tests show no significant change in subordinate aggression rates towards dominants performing any activity. By contrast, dominants are significantly less likely to initiate aggression towards grooming, inspecting or walking subordinates after egg removal ($t_{24} = 2.186$, 2.232 and 2.334 , respectively). (All aggression-rate data were checked for normality prior to analysis.)

remaining colonies were accidentally destroyed before they could be genetically analysed.

3. RESULTS AND DISCUSSION

Although the overall weighted aggression rates do not significantly change after egg removal within the classes of dominant and subordinate wasps (respective Wilcoxon signed-rank tests: $Z = -0.982$, n.s. and $Z = -1.278$, n.s.), the relative change in aggression after the manipulation is highly significant. Before egg removal the subordinates initiate 34.2% of aggression. Afterwards, this rises to 44.7% (Wilcoxon signed-rank test: $Z = -2.892$, $p = 0.004$).

Although consistent with the results of Reeve & Nonacs (1992, 1993, 1997), these results are confounded by aggression rates varying significantly across activities (figure 1). Indeed, movement is the best predictor of receiving aggression: moving wasps are more likely than inactive wasps to draw aggressive reactions from others (table 1). Interestingly, our manipulation affects activity patterns only in dominant individuals (figure 2). After manipulation, dominants move across the nest significantly more and are inactive significantly less than before egg removal. Considering that the manipulation suddenly

created a large number of empty cells, such an increase in exploratory behaviour by dominants is not surprising. Thus, dominants decreased those activities least likely to draw aggressive acts and increased those most likely to draw aggressive acts. As such, aggression rates cannot be compared across observation periods without accounting for individual activity profiles. Examining the effect of the manipulation by activity pattern reveals that, contrary to previous results, subordinates do not increase rates of aggression towards dominants, and dominants appear to decrease significantly aggression towards moving subordinates (figure 1).

A decrease in aggression by dominants in response to their sexual eggs disappearing is inconsistent with a concessional OSM that predicts punishment for cheating (Reeve & Nonacs 1992), with a competitive OSM that postulates that aggression increases reproduction (Tibbetts & Reeve 2000; Reeve & Keller 2001) and with a cooperator-value OSM that predicts a decreased tolerance of subordinates owing to the imminent maturation of workers (Reeve & Nonacs 1997). However, rather than following from any ultimate evolutionary explanation, the decrease in aggression by dominants may instead result from a proximate effect of the experimental protocol. Subordinates and nests were physically handled immediately prior to observation. This, plus the disappearance of eggs, may increase the motivation for subordinates to remain on the nest (e.g. for defence against a perceived increase in predation risk) rather than to forage. Because the return of a forager initiates a period of high activity (grooming, walking and cell inspection by subordinates) with increased aggressive displays (P. Nonacs, H. K. Reeve and P. T. Starks, personal observation), the overall slight decline in aggression by dominants may follow from a reduced rate of foraging by subordinates. Indeed, the data strongly support this hypothesis. First, the proportion of the total time that subordinates are absent from nests declines from an average of 31% to 6% (Wilcoxon signed-rank test: $Z = -3.111$, $p = 0.002$). Second, there is significantly reduced dominant aggression correlated with decreases in the number of absences by the subordinates (table 1).

Aggression between wasps is predicted by OSMs to reflect the prevailing social context of the group. Hence, the aggression between dominants and subordinates before manipulation and the change in aggression following manipulation should correlate with specific between-nest differences. However, all the factors that we could measure that are relevant to OSMs had no significant relationship with aggression (table 1). These include: (i) size differences between wasps (related to the ability to compete or punish cheating; Reeve & Nonacs 1997; Reeve 2000); (ii) absolute nest size or size per wasp (productive nests allow more competition; Cant & Johnstone 2000; Reeve & Keller 2001); (iii) number of eggs removed (degree of cheating; Reeve & Nonacs 1992); (iv) number of pupae (decreased relative value of subordinates or increased group productivity relative to solitary productivity; Reeve & Nonacs 1997; Reeve 2000); and (v) genetic relatedness (closer kin may tolerate higher levels of aggression and reproductive skew; Reeve *et al.* 2000). The lack of an effect of any single factor can be reconciled with OSMs because no one factor always predicts an effect

Table 1. Spearman's correlation results of potential factors affecting aggression on *Polistes fuscatus* nests. (Aggression is calculated as a rate per minute during the time that two wasps spend together on the nest. In all cases, aggression rate is a measure weighted by the severity of acts.)

first variable	second variable	<i>r</i>	<i>n</i>	<i>p</i>
relationships predicted by activity levels				
subordinate:				
percentage inactive ^a	dominant aggression ^a	-0.572	25	0.0051
percentage groom and construct ^a	dominant aggression ^a	0.725	25	0.0004
percentage walk and inspect ^a	dominant aggression ^a	0.522	25	0.0106
aggression before	aggression after	0.424	25	0.0378
dominant:				
percentage inactive ^a	subordinate aggression ^a	-0.524	25	0.0103
percentage groom and construct ^a	subordinate aggression ^a	0.453	25	0.0268
percentage walk and inspect ^a	subordinate aggression ^a	0.533	25	0.0090
aggression before	aggression after	0.416	25	0.0415
aggression after - aggression before (subordinate)	aggression after - aggression before (dominant)	0.898	25	< 0.0001
number of absences after - number of absences before (subordinate)	aggression after - aggression before (dominant)	0.576	25	0.0048
relationships predicted by OSMs				
dominant size - subordinate size	percentage of aggression initiated by subordinate ^{a,b}	0.208	19	n.s.
	change in percentage of aggression initiated by subordinate ^b	-0.040	19	n.s.
nest size (number of cells)	percentage of aggression initiated by subordinate ^{a,b}	-0.005	24	n.s.
	change in percentage of aggression initiated by subordinate ^b	-0.062	24	n.s.
nest size per wasp	percentage of aggression initiated by subordinate ^{a,b}	0.016	24	n.s.
	change in percentage of aggression initiated by subordinate ^b	0.098	24	n.s.
number of eggs removed	change in percentage of aggression initiated by subordinate ^b	0.029	24	n.s.
nest maturity (number of pupae)	percentage of aggression initiated by subordinate ^{a,b}	0.118	24	n.s.
	change in percentage of aggression initiated by subordinate ^b	-0.074	24	n.s.
genetic relatedness	percentage of aggression initiated by subordinate ^{a,b}	0.286	8	n.s.
	change in percentage of aggression initiated by subordinate ^b	-0.238	8	n.s.

^a Activity states (as percentages of the total time wasps spent on the nests) and aggression levels are for the observation before the experimental manipulation.

^b Statistics are given only for aggression summed across all activities. The first variable also had no significant effects on the percentage of aggression when it was split by activity. All non-significant (n.s.) relationships are at $p > 0.35$.

under all potential social contexts (Johnstone 2000; Reeve & Keller 2001). However, *all* five factors having no measurable effect strongly suggests a failure of OSM assumptions.

In contrast to OSM variables, changes in activity profiles are strong predictors of aggression levels. Before manipulation, the rate of aggression received by dominants and subordinates is a negative function of the time spent inactive and a positive function of the time spent moving. Another strong predictor of a given wasp's aggressive behaviour is the behaviour of its nest-mate. If, after manipulation, dominants increase or decrease their aggression, subordinates tend to do likewise (table 1). Although causation cannot be inferred from this relationship, an interaction between wasps is present: taken alone,

the aggression levels of subordinates and dominants before manipulation are much weaker predictors of their aggression levels afterwards.

Although darts, lunges and bites may express aggression in *P. fuscatus*, their rates do not change as predicted by models that assume that they function to affect or respond to reproductive allocations. Alternatively, they may serve as activity regulators (Reeve & Gamboa 1987) or indicators of wasp physical condition. Strassmann (1993) proposed that the increases in subordinate aggression observed by Reeve & Nonacs (1992) were challenges to dominants perceived as weak because of many egg-less cells. This explanation may be wrong in its specifics because no increase may have happened in that study (see also Reeve & Nonacs 1993). Nevertheless, the general

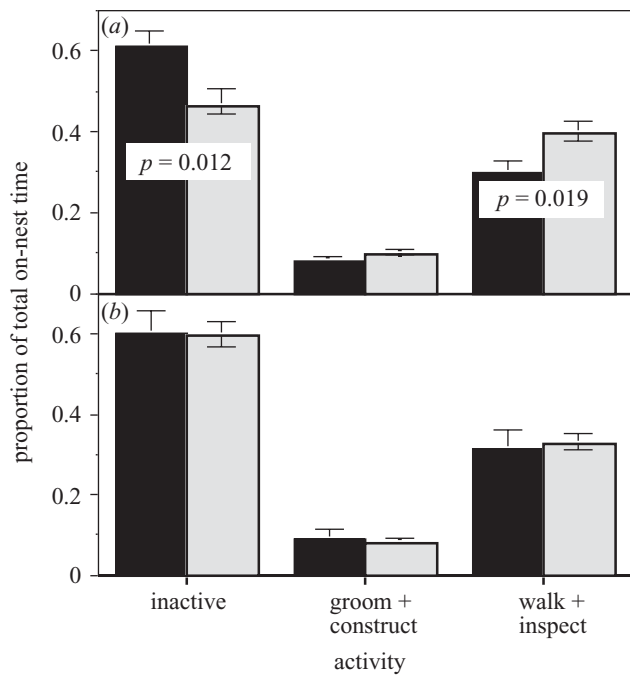


Figure 2. The proportions of time (\pm s.e.) wasps spend in various activities on nests. (a) Dominants spend significantly more time inactive before (black bars) than after (grey bars) egg removal (matched-pair t -test: $t_{18} = 2.789$). Conversely, dominants significantly increase high-movement activities such as walking and inspecting after egg removal ($t_{18} = 2.580$). (b) Subordinate activity proportions are not significantly changed by manipulation. (All activity data were checked for normality prior to analysis.)

principle may have merit. Wasps may probe each other with relatively low-cost behaviours. If a wasp fails to respond appropriately, this may stimulate escalation, particularly from subordinates that perceive opportunities for dominance reversals (Seppä *et al.* 2002). Certainly this possibility requires further experimental investigation.

The above hypothesis suggests that darts, lunges and bites impose a relatively low cost on wasps, but this has not been demonstrated. Tibbetts & Reeve (2000) proposed that these behaviours are energetically costly and that dominants are always close to the maximum that they can expend on aggression. This conclusion rests on the observation that only dominant aggression rates are positively temperature dependent and only during the hotter times of the year. For a poikilothermic wasp, however, it is likely that darts and lunges are energetically trivial in comparison with flying and foraging. The costs of physical damage are likely to be minimal: we did not observe injuries as a result of darts, lunges or bites in either this study or the previous ones. Moreover, these interactions never escalated into fights, although such fights are common when colonies are being initiated or when resident wasps are expelling potential usurpers (Reeve 1991). Other circumstantial evidence also suggests that these acts are not costly. A high cost would predict that peaceful groups have larger nests than aggressive groups (i.e. saved energy can be devoted to increasing productivity). Our study found no relationship between nest cell number per wasp prior to egg removal and the aggression rates of dominants, subordinates or summed for both (all correlations with $p > 0.4$). This comparison, however, measures

aggression on one day and may not reflect a long-term average. A potential correlate of long-term aggression is wasp size difference. Groups with larger size differences may function better because less aggression is needed over the season to maintain dominance (Nonacs & Reeve 1995). Size differences were standardized across nests with differing numbers of wasps by calculating coefficients of variation (CVs) in wasp weight per nest. The sizes of nests do not significantly correlate with these CVs (Spearman's $r = 0.006$, n.s.). Thus, there is little evidence in this study to suggest that darts, lunges and bites are costly.

Several previous studies have found changes in aggression over time or in response to experimental manipulation (table 2). These results have been interpreted as supporting OSMs. In all cases, however, an alternative explanation is that differences in aggression levels are a by-product of changes in activity patterns. Unfortunately, the results of our previous studies (Reeve & Nonacs 1992, 1997) cannot be reanalysed because most nests were not videotaped and aggression cannot be subdivided by activity category. Nevertheless, there is an intriguing similarity. Although we could not measure time spent per activity, we did record the number of times wasps engaged in high-movement activities such as patrolling or inspecting cells. Indeed, the change in the rate of aggression of one wasp is strongly correlated with the change in the rate of movement activities by the other wasp (Spearman's $r = 0.591$, $n = 22$, $p = 0.007$). The combination of this similarity and the replication of the previous results when individual activity levels are not controlled for leads us to believe that the earlier experiments did not produce any changes in aggression supportive of OSMs.

An alternative hypothesis is that the total number of aggressive acts functions to set the level of reproductive skew and that changes in activity patterns proximately increase aggression by subordinates. This, however, is a very indirect hypothesis as it proposes that subordinates increase their aggression rates not by modulating their own behaviour, but in expectation that dominants will increase activities that stimulate attack. Given the lack of unequivocal evidence in *P. fuscatus* that aggression gains immediate reproduction or correlates with any factor OSMs predict to be important, it is more parsimonious to conclude that what is called aggression in this species does not directly affect reproductive partitioning.

It is important to note that our conclusions are specific to observations of 'aggressive' interactions between individuals that have already been cooperating for an extended period of time. When paper wasps first initiate nests and establish a dominance hierarchy, serious fights with grappling and attempts to sting are common (Reeve 1991; P. Nonacs, H. K. Reeve and P. T. Starks, personal observation). Because it is at this point that reproductive dominance is first established, this early aggression may indeed decide the level of skew observed later in the colony cycle. To date, no study has correlated the aggression levels when hierarchies form to the skew later expressed. Thus, the proximate mechanism of how skew is set and changed in polistine wasps remains to be discovered. Indeed, all studies that use aggression or other behaviours

Table 2. Previous studies of aggression in polistine wasps.

(As the studies do not indicate the constancy of activity patterns, the alternative explanation cannot be either supported or rejected.)

observation	OSM explanation (from Tibbetts & Reeve (2000) or Reeve & Keller (2001))	altered-activity-pattern explanation
aggression increases over the season until workers emerge; dominants increase the proportion of acts they initiate (Gamboa & Stump 1996; Reeve <i>et al.</i> 1998 <i>b</i> ; Tibbetts & Reeve 2000)	skew in reproduction increases, with aggression being the proximate mechanism for the shift	nests later in the year are larger and contain older brood more demanding of food, and temperatures are higher; all factors increase activity, particularly in subordinates
aggression towards subordinate declines after worker emergence (Savoyard & Gamboa 1999)	nests with workers are closer to saturated group size, reducing selfishness windows	workers take over foraging duties and subordinates become less active
removal of low-ranked individuals (foragers) increases aggression between dominant and higher-ranked wasps (Gamboa <i>et al.</i> 1990)	nests are now further from saturated group size, increasing selfishness windows	higher-ranked wasps now have to forage more, which increases their activity levels and the number of times they come and go from the nest
aggression is higher in low-skew smaller groups (Field <i>et al.</i> 1998)	small groups are further from saturated group size, increasing selfishness windows	nest size increases with wasp number, but at a declining rate, which suggests that there is a higher <i>per capita</i> activity level on smaller nests
aggression is higher on larger more productive nests (Reeve & Keller 2001)	skew in reproduction is greater on larger nests, with aggression being the proximate mechanism for the shift	larger nests require more foraging, feeding of larvae and movement across the nest
only the dominant's aggression rate is temperature sensitive, and only late in the season (Tibbetts & Reeve 2000)	the dominant is close to its physiological maximum in terms of aggressive acts and can only increase these with warm temperatures; the increase correlates with increased skew; subordinates are showing behavioural restraint in their aggression	the subordinate's foraging rate is physiologically constrained; in hotter weather the subordinate can forage more; this higher activity stimulates more aggression from dominants
dominants exhibit more aggression on nests with less food sharing (Tibbetts & Reeve 2000)	lowered food sharing equates with increased reproductive competition and therefore increased aggression	food sharing preoccupies the dominants with feeding larvae and thus reduces responses to subordinate movement; with no sharing, subordinates move rapidly between cells when feeding larvae and the activity draws aggression
removal of early eggs reduces dominant aggression but has no effect on subordinates (Reeve & Nonacs 1997)	dominant is unwilling to engage in reproductive competition when subordinates still need to be offered staying incentives	manipulation and empty cells reduce subordinate foraging behaviour, which results in lower overall activity
removal of pupae (present at the same time as sexual eggs) reduces dominant aggression but has no effect on subordinates (Reeve & Nonacs 1997)	removal increases subordinate value because worker emergence is now considerably delayed	manipulation and empty cells reduce subordinate foraging behaviour, which results in lower overall activity

as metrics for testing skew models must demonstrate, rather than assume, a link to reproductive partitioning.

Finding proximate mechanisms for setting skews in paper wasps is important because many qualitative features of their reproductive partitioning support OSM predictions. Observed apportioning of reproduction across wasps according to genetic relatedness, changes in reproductive skew over time and significant correlations between skew and productivity are consistent with OSM predictions and not readily consistent with other evolutionary models (Reeve *et al.* 2000; Nonacs 2001, 2002; Reeve & Keller 2001). In conclusion, if cooperation evolves through the dynamics of an OSM, then there must

be a proximate mechanism by which the transactions are consummated. Finding that mechanism will both be a confirmation of OSMs and provide a useful tool to discriminate between the many variants of OSMs.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.